Competitive Co-Existence:
Maintenance of Interacting Associations of the Sea Mussels *Mytilus edulis* and *Mytilus californianus*

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(8 Text figures)

INTRODUCTION

IN SPITE OF THE LARGE AMOUNT of practical and theoretical work on interspecific competition which has been produced since DARWIN'S **Origin of Species** (1859), few field experimental investigations of the process have been performed. The work of CONNELL (1961a, 1961b) provides notable relief from this lamentable state of affairs. Most studies have demonstrated that the competitive exclusion principle as outlined by HARDIN (1960) provides an appropriate model to account for the fact that one or the other of any pair of competing species eventually eliminates its opponent in a homogeneous laboratory universe of limited extent. While it is true that the process involved may take considerable time [FRANK (1952, 1957); PARK (1948, 1954)], involving several generations of the animals concerned [see MILLER (1969) for a discussion of this point], and perhaps extending over a longer time interval than most natural habitats would last in an unaltered state, nevertheless the outcome is always predictable, even if prior identification of the victor is uncertain [NEYMAN *et al.* (1956)]. Mathematical models of competition utilizing the concept of a persistent advantage accruing to one species with consequent disadvantage to the other [GAUSE (1934); GAUSE & WITT (1935)] or stochastic versions of this process [BARTLETT (1960); LESLIE (1962)] indicate a similar outcome provided only that resource limitation is postulated. AYALA (1968, 1971) provides one of the few examples of a laboratory system wherein competitive exclusion does not take place (see later).

It is obvious that organisms overlap in their requirements for both physical and biological resources, and the extent to which competitive interactions are realized in nature between sympatric species is endlessly debated. The principal argument advanced to substantiate absence of such competition is that differences allowing for separation of species are sufficient to permit co-existence by enabling them to avoid competition for limited resources. COLE (1960), in fact, criticizes the stress HARDIN (1960) places on the competitive exclusion principle because it leads to such circularity in interpreting field results. DE BACH (1966) admits to the existence of transient competitive displacement which may hold sway for undefined but definite periods following range extensions or the artificial introduction of organisms into new habitats. The mechanism of competitive displacement is presumed to result in organisms spacing themselves apart from one another with respect to their demands for potentially limited resources, such that they fail to effectively compete with each other. DE BACH (*op. cit.*) goes to considerable lengths to define "ecological homologues" as species having the same "ecological niche"; he also states that species having different ecological niches are able to co-exist indefinitely in the same habitat. Unfortunately, these definitions are applied by pointing out that cases of co-existence pertain only to species which are not ecological homologues. Since all species differ in some respect to each other, this is of little help, particularly when it is indicated that "niche overlap" need only be partial in the sense that "niches do not have to be identical in all respects for competition and displacement to occur." The problem of circularity exists throughout DE BACH'S (*op. cit.*) review.

HARPER *et al.* (1961) postulate that continued cohabitation of competing species is possible only if species dif-

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fer in such a way that their populations become independently controlled, and that apparent cohabitation in nature presents a challenge (to the biologist) which can be met by showing: (a) that apparent cohabitation is spurious because there is really a previously undetected heterogeneity in the habitat, in space or time, so that the populations do not really cohabit; (b) the cohabitation is transient and does not represent a stable state; (c) the populations or species concerned do not have controlling factors in common. Harper *et al.* (*op. cit.*) further state that it is clear from mathematical models (Williamson, 1957) that two non-interbreeding populations or species are unable to exist together in equilibrium if they hold a controlling factor in common.

It is, however, likely that heterogeneity is always present in the habitat of organisms engaged in competitive interaction in nature. Since the effects of such heterogeneity are difficult to evaluate in the absence of extensive experimental investigation, a claim which substitutes "heterogeneity" for an understanding of processes involved is of little value. The statement concerning transience is also difficult to evaluate, since it involves setting undefined standards; namely, transient with respect to what? Most ecologists will agree that most population interactions are transient in nature. Thus, transience could relate to a geological time scale or one reflecting the life span of the organism or some lesser interval. Williamson (*op. cit.*) describes a "controlling factor" as one which acts more severely against the individuals of a population when the population increases and so tends to control the population size. Two species are in competition when they have a controlling factor in common, and conversely, if two species are in competition, they have a controlling factor in common. Williamson (*op. cit.*) concludes that two species, each with a constant birth rate and death rate caused only by a single controlling factor acting simply on both of them, cannot coexist. Obviously, this does not mean that the existence of a controlling factor acting on two species precludes co-existence.

It is clear that Darwin (1859) regarded the operation of competitive interactions between organisms as an essential factor promoting evolution: "... as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species or with the physical conditions of life." And later, "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

There is no doubt that competition occurs in natural communities. That exclusion of one species by another in laboratory experiments takes place is also a fact. It is, therefore, important to enquire into the conditions under which co-existence may be maintained, in spite of competitive interactions between species. What are the factors governing degree of overlap that may exist between species? An attempt to answer such questions underlies the development of this work.

Several authors have envisaged situations wherein the co-existence of competing species ["Ecological Homologues," De Bach (1966)] would be possible. Hutchinson (1957) suggests that co-existence might occur if the advantage of one species over the other is continually reversed by habitat variations. Klomp (1961) considers this could occur only if habitat variations were dependent on the numerical ratio of the species involved. I have indicated (Harger, 1970c) that in this system of interacting sea mussels such a possibility exists, in that the effect of wave action on mussel populations varies according to the proportions of the two species constituting the clumps. Pimentel *et al.* (1965) have proposed that structural diversity may allow competitively superior genotypes to evolve in beleaguered populations in response to selection imposed by temporarily successful genotypes of numerically dominant species. Nicholson (1954) accounts for co-existence in regions of species overlap by continual re-colonization from species-specific refuges. Williamson (1957) claims two species may co-exist if they possess two or more "controlling factors" in common. In fact, Williamson (*op. cit.*) considers it likely that survival of both competitors becomes more likely as more variables are considered. Skellum (1951) postulated a method whereby two species in competition may co-exist if one species, the loser in spots seeded by both, nevertheless produces more seeds than the other species, and so it is better able to find new vacant spots. Hutchinson (1957) also points out co-existence may be expected when potential competitors occur at such low densities that competition is not involved.

Sea mussels lend themselves admirably to experimental investigation of competition. In accordance with the suggestions proposed by Park (1962), "they are easily and safely handled, can be readily grown apart and in conjunction with one another, and can be manipulated to grow in different environments." An evaluation of some of the foregoing ideas was sought in a field investigation of factors affecting interaction of *Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837. The first step in this process was to determine whether both competition and co-existence were taking place in natural populations.

Mytilus edulis and *M. californianus* are two species of sea mussel which occur in large numbers on the shores of Southern California. *Mytilus edulis* attains high population densities in quiet waters, such as those found in harbors, beneath marina floats, etc. Occurrence in this habitat has given rise to the name "bay mussel." This species is, however, not confined to such situations and occurs in considerable numbers, together with *M. californianus* (the "open coast" mussel) intertidally on exposed pier pilings (Harger, 1968), oil rig pilings (Carlisle *et al.*, 1964) and indeed along most of the exposed shore line of Southern California. Stubbings (1954) reports a "world wide" distribution for *M. edulis,* since it is present in both northern and southern hemispheres.

Mytilus californianus is confined in distribution to the west coast of North America, where its range extends from the Aleutian Islands to Isla del Socorro, Mexico (Soot-Ryen, 1955). It occurs principally on exposed shorelines, but may extend into harbors, particularly if the water is generally free from silt and suspended particulate matter. In Northern Washington, for instance, it occurs on the shores of San Juan Island, situated in Puget Sound, midway between the Strait of Juan de Fuca and the mainland, a comparatively protected region characterized by clear water and swift currents. I have found *Mytilus californianus* growing under marina floats in Morro Bay (San Luis Obispo County, California), Santa Barbara Harbor, and in the Ventura Marina (Ventura County, California).

As reported previously (Harger, 1968), both species contribute to the formation of mussel clumps on pier pilings in Southern California. Representation of *Mytilus edulis* in such clumps may vary from a few small individuals to 50% or more by number. Generally speaking, mussel clumps in locations exposed to heavy wave action contain fewer and smaller individuals of *M. edulis* than those in more sheltered situations (Harger, 1970a, 1970c). In conditions of extreme exposure, such as found on the Monterey Peninsula (Monterey County, California), *M. edulis* was entirely absent. However, a surprisingly high representation of *M. edulis* (50% by number) occurred in clumps exposed to moderately heavy wave impact on a pier belonging to the Standard Oil Company at Cayucos Beach, San Luis Obispo County, California (Harger, 1970a).

Small individuals of *Mytilus edulis* also occur on the exposed outer coast of Vancouver Island, British Columbia, at Port Renfrew, indicating that overlap between the two species is not confined to Southern California. The investigation reported here was initiated after I observed both *M. edulis* and *M. californianus* making up large clumps on pilings supporting Ellwood Pier (property of Signal Oil and Gas Company). This pier is located some 14 miles west of Santa Barbara on an open sandy shore. Constructed on steel girders, it extends approximately ½ mile into the sea, from the shallow surf zone to a depth of 40 feet. Mussels were confined in clumps of varying sizes (ranging from a few individuals to large masses over 17 feet in circumference). Maximum vertical extent was 7 to 9 feet (from 1.5 - 2 feet below the extreme high water spring tide mark to the low water mark – 0.0 chart datum).

In all cases the animals were packed closely together (see Harger, 1968 for a description of clump structure). A limited amount of substrate suitable for mussel colonization is available in the intertidal region. Most subtidal surfaces are unsuitable because predation by sea stars (Landenberger, 1967), crabs and fish results in the rapid removal of settling mussels (see also Seed, 1969). This would seem to indicate that space sometimes limits population densities of these animals. The effect of such limitation was particularly noticeable on the pier pilings, most of which were H-beams 9 inches on a side. A large mussel clump, 17 feet in circumference, vertical extent of 9 feet, was approximately 28 inches thick from the outside surface to the central piling support. At least 14 or more mussels are piled one on top of the other at this point: all are fastened to the central pillar.

PHYSICAL CHARACTERISTICS OF THE MUSSELS

As might be expected, the two species of mussels are dissimilar in their most easily measured characters. Shells of *Mytilus californianus* are almost always heavier than similar sized shells of *M. edulis* taken in the same place ($p < 0.001$, Harger, 1967, table 4). An exception occurs when old individuals of *M. edulis* occur in exposed situations together with young specimens of *M. californianus*: *M. edulis* shells may then be heavier.

Shells of the two species are different in shape, with *Mytilus edulis* being wider ($p < 0.001$, Harger, 1967, table 5).

Byssal thread material is produced by *Mytilus californianus* in greater quantity than by *M. edulis* ($p < 0.001$, Harger, 1967, table 6). This disparity is reflected by the difference in effort required to remove individuals of the two species from a rock face. *Mytilus californianus* requires greater effort when similar sized mussels are compared (Harger, 1970a).

Shells of *Mytilus edulis* bear few check rings in comparison with those of *M. californianus* (Harger, 1970a);

M. edulis grows to a maximum length of around 12 - 15 cm under favorable conditions, whereas *M. californianus* attains 20 - 25 cm or perhaps more.

Thick shells and strong byssal threads both can be regarded as adaptations to heavy wave shock.

A third species of mussel, *Septifer bifurcatus* (Conrad, 1837), also occurs intertidally on the Santa Barbara coast (rarely on pilings) and is similar physically to *Mytilus californianus* in that it has a thick shell and approximately the same dry body weight, length for length, as the latter species. Also, there is no significant difference between mean shell weight of the two species. Maximum size attained by *Septifer* is 3.4 - 4.5 cm, but effort required to remove individuals from the substratum is greater than that required to remove similar-sized *M. californianus* (Harger, 1970a). The pressure which must be exerted to crush *Septifer* shells is greater than for similar-sized *M. californianus* individuals ($p < 0.001$, Harger, 1967, table 27). *Mytilus edulis* shells were far more brittle than those of either *M. californianus* or *Septifer*.

During June 1965, when the study was initiated at 340 pilings of Ellwood Pier, approximately $\frac{1}{3}$ were without mussels. The mussel clumps themselves were comprised principally of *Mytilus californianus; M. edulis* made up from 10% to 50% (by numbers) of half the clumps, with remaining populations trailing off to effectively zero representation (there were, however, almost always a few individuals of *Mytilus edulis* in "pure" *M. californianus* clumps).

If competition occurs between the two species, evidence of this should, presumably, be present within the clumps. Accordingly, several populations were dissected and carefully examined. Clumps of differing sizes were chosen, some composed of both species and others almost entirely of *Mytilus californianus*. Before removing samples from pilings, the outside mussels were sprayed with white enamel paint, so providing an objective character by which individual mussels could be identified as to position occupied in the clumps. Animals completely or partly covered with paint were recorded as "outside," and the rest as inside mussels. In mixed aggregations most of the *M. edulis* occur on the outside of the clumps; juvenile *M. edulis* (up to 2.5 cm in length, measured from the posterior hinge to the anterior siphon region) tend to be found on the outside of the clumps, while juvenile *M. californianus* tend to occur within the body of the clumps (Harger, 1968). Mussels at the bottom of the clumps are longer than those growing at the top, and overall, *M. californianus* tends to be larger than *M. edulis* (Figure 1).

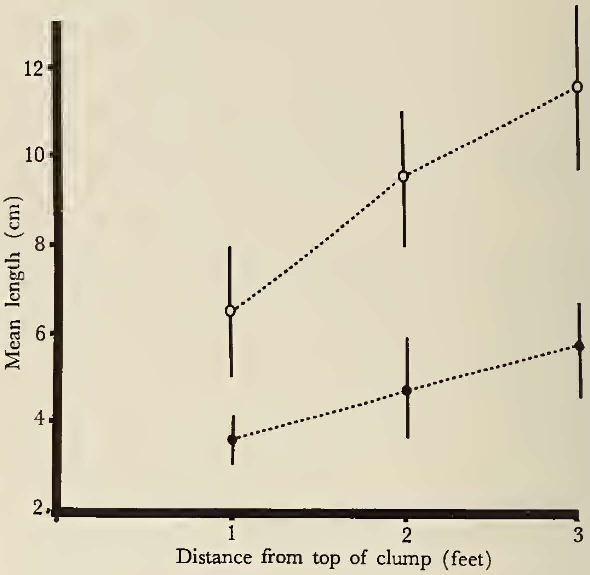

Figure 1

Relationship between height on mussel clump and mean size of mussels. One standard deviation is plotted each side of the mean.

● *Mytilus edulis*

○ *Mytilus californianus*

Evidence for competition seemed to be present in both mixed and pure mussel clusters. Those mussels taken from the inside of clumps were very different in appearance from mussels growing on the outside. Individuals of *Mytilus edulis* tended to have thick, heavy shells ($p < 0.001$, Harger, 1967, table 10) and many "check rings" ($p < 0.001$, Harger, *op. cit.*, table 11) (see Harger, 1970a for a discussion on formation of check rings); in addition, compared with individuals taken from the outside clumps, those inside were often found deformed and twisted and had lower body weights ($p < 0.001$, Harger, 1967, table 12). Shells from dead *M. edulis* were common throughout the clumps, particularly on the inside; they were also quite common within the clumps which were principally comprised of living *M. californianus* (Harger, *op. cit.*, tables 13 and 14).

Mytilus californianus taken from inside clumps tended to show differences from outside mussels paralleling those for *M. edulis*. However, shell weights of inside mussels were not significantly higher than those from the outside; in fact, the reverse tended to be true ($p < 0.05$, Harger, 1967, table 15). For those on the inside, check rings were more numerous (Harger, 1970a) but shells retained their normal shape. Dead *M. californianus* shells from inside the aggregations were very rare and were almost absent from the outside regions.

One explanation for this disparity in frequency of dead shells from the two species might be that *Mytilus californianus* dissolves in sea water faster than *M. edulis.* Accordingly, several batches of shells were immersed mixed with living mussels in cages placed 2 feet below low water. Results indicated that *M. edulis* shells (4 - 5 cm long) disintegrated in 2 to 4 months of continual immersion in sea water, while those of *M. californianus* were still quite solid after 6 months' immersion, finally crumbling at 9 to 12 months. It seems unlikely, therefore, that shells from dead *M. californianus* could have dissolved within the clumps, leaving only *M. edulis* shells.

An extensive investigation was made into the relationship between position occupied within clumps and body weight of mussels. Sampled mussels were heated for a few minutes at 90° C in water (this caused the shells to gape open, allowing easy removal of the "body" and adductor muscles; the heating process did not significantly alter body weight of the animals). The bodies were then dried for at least 24 hours at 80° C in a forced-draught oven and were then weighed.

The effect of intertidal position was most noticeable in *Mytilus edulis.* Mussels growing on the clump tops, *i. e.,* high up in the intertidal, were consistently lighter than those growing at the bottom ($p < 0.01$, Harger, 1967, tables 18, 19). This was not true for *M. californianus*; generally, there appeared to be no difference in body weight between specimens taken from the top or bottom of the clumps for this species. However, considerable variation existed here, but there was no consistent trend; sometimes an individual clump had heavier mussels on the top portion, while other samples indicated heavier mussels on the bottom.

Differences in body weight between mussels growing inside clumps and those growing on the outside showed a similar trend for both species, those on the inside were lighter than those on the outside. For *Mytilus californianus* this reduction was significantly greater for mussels growing in the center of a large clump (12 feet in circumference) than for a medium-sized clump (8 feet in circumference) ($p < 0.01$, Harger, 1970, table 20).

Small *Mytilus californianus* (2 - 5 cm) inside clumps contain approximately the same amount of meat as those outside. Larger individuals have significantly lower body weights inside than outside clumps, probably because the large mussels tend to press against each other, while the small ones presumably fit within the interstices.

Only one medium-sized clump containing both species was investigated fully, but small and large *Mytilus edulis* were affected to the same degree (Harger, 1967, table 12).

Evidence most suggestive of competition occurring within mussel clumps was provided by the presence of numerous shells from dead *Mytilus edulis* within aggregations of living *M. californianus* only. These shells were inclined to be even heavier and more "robust" looking than shells taken from *M. edulis* individuals growing within mixed clumps, or those growing in relative freedom outside ($p < 0.001$, Harger, 1967, table 21).

The preceding observations led to the following hypothesis: *Mytilus edulis* settles on the outside of the clumps or throughout the clump matrix. Subsequently, with growth of *M. californianus,* pressure is exerted on *M. edulis* individuals within the clumps; these are eventually crushed or in some way bound by byssal threads and jammed together so that they die. Since *M. californianus* grows to a larger size than *M. edulis,* individuals of *M. edulis* on the outside of the clump would eventually be incorporated into the clump matrix where a similar fate would befall them.

EXPERIMENTAL METHODS

The following description of experimental techniques used to investigate competition between the two species of mussels is taken largely from Harger, 1970b.

Mussels used in experiments were placed in wire mesh cages suspended intertidally at various heights from cross-girders at Ellwood Pier or from marina floats in Santa Barbara Harbor. Cages were cylindrical in shape (diameter 7 inches or 17.78 cm, height 8½ inches or 21.5 cm) constructed from galvanized hardware cloth. Components (wire sections, etc.) used in cage constructions were laced together with braided nylon cord and the entire unit was coated with epoxy resin. This coating served to give rigidity to the nylon binding and at the same time to cut down any leaching of zinc ions which might affect enclosed mussels. A log normal distribution of mussel lengths was chosen to represent mature mussel populations, since this was similar to the distribution of *Mytilus californianus* within clumps on Ellwood Pier (Harger, 1968). The mussels used ranged in length from 2.5 cm up to 10 cm (for size classes and frequencies, see table 1, Harger, 1970b). *Mytilus californianus* individuals occurring within clumps are often much larger than 10 cm, but this tends to be the upper size limit for *M. edulis.* A log normal distribution most accurately mimics that of *M. californianus* in natural clumps (Harger, 1968), and although the distribution of *M. edulis* tends to be normal, or bimodal normal if both juveniles and adults are present, it seemed advisable to use an identical size distribution for both species in order to be sure of eliminating any effects which might arise as the result of size differences.

Cages containing populations of mature mussels were constructed from ½-inch (1.27 cm) aperture hardware cloth and a total of 90 mussels was placed within each cage (equal numbers of the two species for mixed populations). Individual mussels used in the experiments were marked in the following manner: after drying, a small patch was scoured on the shells with sandpaper, code numbers were written on the roughened surface with white ink, and a small drop of clear epoxy resin was placed over the symbols and allowed to harden overnight.

The maximum length of each animal was recorded in centimeters (accurate to 2 decimal places), between the anterior hinge and the posterior siphon regions at the commencement and conclusion of the experiment (mussels were removed from water for approximately 12 to 24 hours for marking, etc., and mortality ranged between 10 and 15% as a result of this procedure).

All mussels used in the experiments were taken from clumps at Ellwood Pier no more than one day before marking. Before and immediately after marking the animals were kept in running (non-recirculating) sea water. Laboratory containers were well aerated and mussels spent a maximum of 3 days between removal from the pier clumps and replacement at the pier within experimental cages.

Two methods were used to study supposed competitive processes occurring between the two species of mussels. The first involved mixing populations of mussels with approximately the same size distribution as found within the mussel clumps on the pier. The second method involved using groups of juvenile mussels (1.5 - 2.5 cm long) to establish the effect one species might have upon the other when both were newly settled.

Experiments with Artificial Mature Mussel Populations

An experiment using a 3-way factorial design was set up involving 2 species, 3 intertidal levels, and 4 treatments. The top, middle, and bottom intertidal levels corresponded to the top, middle, and bottom of the mussel clumps occurring on Ellwood Pier pilings (Harger, 1968). The 4 treatments consisted of different arrangements of mussels within cages: Treatment 1 consisted of surrounding one species in the center of the cage by the other species; treatment 2 - the reverse; treatment 3 consisted of mixing individuals of both species as evenly as possible; and treatment 4 of *Mytilus edulis* and *M. californianus* alone. This experiment was initiated before I was aware of behavioral differences which exist between the two species (Harger, 1968). Briefly, *M. edulis* individuals react to pressure imposed upon them by crawling against such pressure, whereas *M. californianus* react slowly or not at all. Thus, the first 3 treatments probably became identical since *M. edulis* tended to arrange itself on outer surfaces of the caged clumps. Only cages containing pure *M. californianus* and pure *M. edulis* (3 replicates of each) were run at the mid-intertidal level. All other treatments within the design were replicated 5 times.

An extension of this experiment consisted of setting up 2 replicates of the following 3 treatments in Santa Barbara Harbor: evenly mixed *Mytilus edulis* and *M. californianus*; pure *M. edulis*; and finally, pure *M. californianus*. Cages were suspended from marina floats in such a way as to be approximately 1 foot (30 cm) below the water surface at all times.

The complete experiment was started during August 1965; at Ellwood Pier, 3 of the aforementioned 5 replicates were left in the sea for 6 months before removal (including the mid-tide cages) and the remaining 2 replicates were withdrawn after one year.

After determining whether individual mussels were alive or dead, I recorded for each: growth increment, new check rings, and position within the mussel clumps (*i. e.*, inside or outside). The numbers of new recruit mussels within the cages were also noted. When the 12-month cages were recovered, dry body weights and dry byssal weights were recorded separately for each mussel, as were the number and species of crabs present in each cage.

Experiments with Juvenile Mussel Populations

Competition between juvenile mussels (1.5 - 2.5 cm long) involved 3 treatments, each replicated twice: (a) pure *Mytilus edulis* (200 individuals): (b) pure *M. californianus* (200 individuals); (c) *M. edulis* mixed evenly with *M. californianus* (100 individuals of each species). Individual animals were not marked, all were measured at the start and at each inspection. Cages containing them were plastic kitchen colanders (10 inches or 25.4 cm in diameter) placed face to face and lashed together round the edges. The maximum diameter of holes in the colanders was ¼ inch (0.63 cm). All cages were first suspended from Ellwood Pier in October 1965 at the low intertidal position only. The first 3 inspections were made at intervals of one month. Thereafter, in order to reduce effects of disturbance that might influence the outcome of the experiment, the interval was increased to 2 months for the next 2, and to 4 months for the last 3 inspections. In all, a total of 19 months' growth was recorded. A further experiment using juvenile mussels was set up during January 1966 to check growth and the effects of competition in both rough and calm waters. The 2 locations used for this experiment were Ellwood Pier (rough water) and Santa Barbara Harbor (calm water). The experimental populations (200 individuals) were set up in wire hardware cloth cages ($\frac{1}{4}$-inch or 0.63 cm aperture) and positioned in the same manner as previously reported, at the pier (lowest level) and the harbor. In the harbor 3 treatments (pure *Mytilus edulis*; pure *M. californianus*; and both in even proportion) were the same as reported for the previous experiment, together with a parallel set at Ellwood Pier. Two additional treatments (*M. edulis* and *M. californianus* in the ratio of 3:1 and the reverse) were also used at the latter site. These were designed to investigate the effect of differing initial proportions of the 2 species on the outcome of the competitive process. A checking interval of 4 months allowed time for undisturbed growth, and the experiment was maintained until September 1966 at Ellwood Pier and May 1967 at Santa Barbara Harbor.

RESULTS
of COMPETITION EXPERIMENTS

Growth

Information concerning growth characteristics of both species was obtained from the previously described experiments and is presented in Harger (1970b). In summary:
(1) At Ellwood Pier (rough water), populations of *Mytilus californianus* grew faster than those of *M. edulis* (although at low intertidal levels small individuals of *M. edulis* grow faster than *M. californianus* of equivalent size).
(2) In Santa Barbara Harbor (quiet water), *Mytilus edulis* populations showed more growth than *M. californianus* populations.
(3) Growth of both species is reduced at high intertidal levels from that shown at low intertidal levels. Growth of small individuals of *Mytilus edulis* decreases more sharply from low to high intertidal levels than that of *M. californianus*. Growth of large mussels of both species is reduced by the same degree from low to high intertidal levels.
(4) The greatest overall growth for both species occurred at Ellwood Pier.

At the lower clump levels *Mytilus edulis* grew at a greater rate than *M. californianus* for approximately the first year; *i. e.,* until *M. edulis* reached a length of 5 - 5.5 cm; thereafter, growth fell off and almost ceased by the time the mussels reached a length of 10 cm. Growth of *M. californianus* did not decline appreciably until at least 15 cm was reached (2 - 3 years), and exceeded growth of *M. edulis* after a length of about 6 cm was reached; the difference between the two became increasingly great thereafter. At the upper clump levels growth rate of *M. edulis* never exceeded that of *M. californianus.*

Competition Experiments Involving Small Mussels at Ellwood Pier

The first inspection (November 1965) of the experiment set at Ellwood Pier in October 1965 disclosed crawling behavior of *Mytilus edulis* (Harger, 1968), which enabled it to arrange itself on the outside of mixed species clumps. The experiment was initiated with *M. edulis* populations significantly smaller than the *M. californianus* populations (Harger, 1970b, figure 11). After one month's growth all the *M. edulis* populations taken together were significantly larger than *M. californianus* ($p < 0.001$, Harger, 1967, table 28). The pure *M. edulis* populations at this time were larger than the pure *M. californianus* clumps ($p < 0.001$, Harger, *ibid.,* table 30). After 2 months' growth (December 1965), the above statement was still true, but by this time *M. edulis* populations grown in pure culture were significantly smaller than *M. edulis* populations grown in competition with *M. californianus* ($p < 0.001$, Harger, *ibid.,* table 31). Presumably this was because the *M. edulis* individuals in the mixed cages were able to arrange themselves on the outer regions of the clumps with *M. californianus* in the center. *Mytilus edulis* consistently on the outer regions of mixed clumps grew more than populations from the pure *M. edulis* clumps, a proportion of which were always on the inside, suffering consequent growth reduction.

In March 1966, after 5 months' growth, a difference between the 2 treatments of *Mytilus californianus* became apparent. Those populations growing in competition with *M. edulis* were significantly smaller than those growing in pure clumps ($p < 0.05$, Harger, 1967, table 32). This difference increased at subsequent stages, then decreased. I concluded, therefore, that the presence of *M. edulis* growing on the outside of the *M. californianus* populations resulted in decreased growth of the latter species.

The experiment was maintained for 19 months. In May 1966 (after 7 months) the clumps were placed in large cages (diameter 9.5 inches, height 12 inches) made of $\frac{1}{2}$-inch aperture hardware cloth. Sometime after September 1966 the two cages containing pure *Mytilus edulis* were lost in a storm. One cage containing pure *M. californianus* was lost sometime after January 1967.

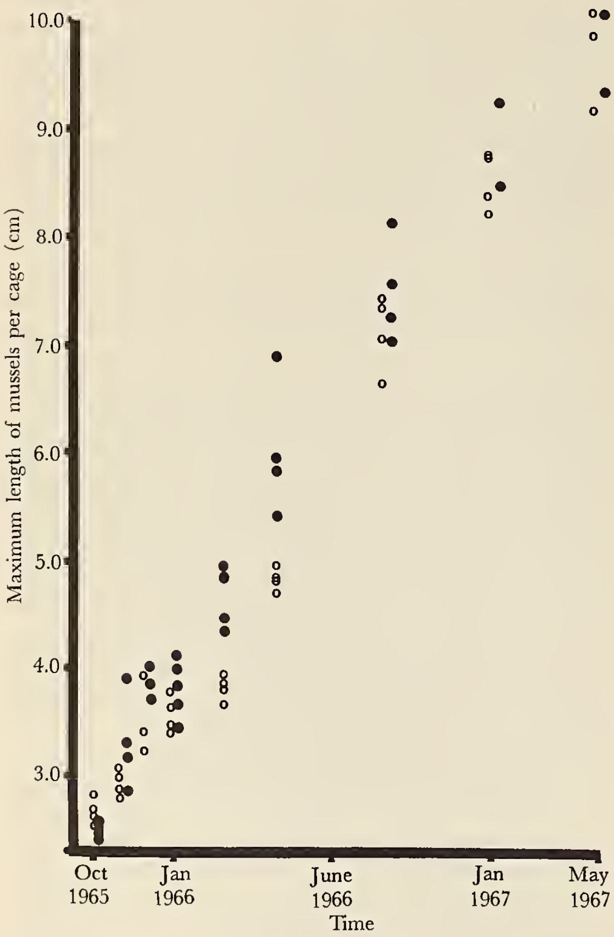

Figure 2

Maximum size of mussels occurring in each cage throughout duration of competition experiment involving juvenile individuals.
● *Mytilus edulis*
○ *Mytilus californianus*

At the last reading (May 1967) the following size relationships were observed. Two populations of *Mytilus edulis* from the mixed cages together were significantly larger than the remaining pure *M. californianus* population plus those from the mixed cages ($p < 0.001$ Harger, 1967, table 33). There was still a slight difference between *M. californianus* grown alone and those grown in competition with *M. edulis* ($p < 0.05$), but by this time the size difference between the two species was almost eliminated. To illustrate this point further, Figure 1 records the size of largest mussels found per cage at each check point. Only at the first and last check points is *M. californianus* as large as *M. edulis*.

This experiment indicated no difference in mortality for either species between mussels growing in mixed or pure species cages. The reshuffling following each interruption for purposes of measurement may have contributed to this by relieving mortality factors such as crab predation and mutual interference.

Crawling behavior provides the initial competitive advantage which *Mytilus edulis* enjoys over *M. californianus*. The presence of *M. edulis* outside of mixed clumps tends to inhibit the growth of the enclosed *M. californianus*. However, evidence from pure *M. californianus* clumps indicates that this species inhibits its own growth to a greater extent than the presence of *M. edulis* does.

Five months after the start of the experiment it was found that mussels growing inside pure *Mytilus californianus* clumps were significantly smaller than those growing outside of the same clumps ($p < 0.001$, Harger, 1967, tables 34 and 35). Further, *M. californianus* developing inside pure *M. californianus* clumps were significantly smaller than those surrounded by *M. edulis* ($p < 0.001$, Harger, *ibid.*, table 36). It would seem that *M. edulis* inhibits the growth of *M. californianus* in a less efficient manner than *M. californianus* itself does and that the advantage *M. edulis* enjoys is almost entirely due to its crawling behavior. (The effect of enclosure within clumps is discussed below in the case of the adult mussel clumps.)

Results from the competition experiments using small mussel clumps consisting of differing ratios of the 2 species were parallel to those obtained previously. There was no tendency for higher concentrations of *Mytilus edulis* to inhibit the growth of *M. californianus* to a greater extent than that shown by the 1 : 1 ratio. This experiment was, however, influenced by crabs settling in the cages and preferentially attacking *M. edulis*, so that after 8 months all treatments tended to be similar. (This will be discussed in detail in the section dealing with predation.)

At low intertidal levels, there seem to be two immediate advantages possessed by *Mytilus edulis* over *M. californianus*: (1) crawling behavior and (2) initial growth greater than that of *M. californianus*. The first is the only one possessed by *M. edulis* growing at upper clump levels.

When individual mussels in a clump are quite small (2 - 4 cm), the crawling behavior results in a distribution of *Mytilus edulis* which may cut down the available free water supply to those individuals enclosed within the clumps. Small mussels fit together snugly and have very small gaps between them. As small mussels grow, spaces among outside members of the clump increase greatly, allowing mussels which were formerly completely covered to protrude among those outside. Figure 3 records

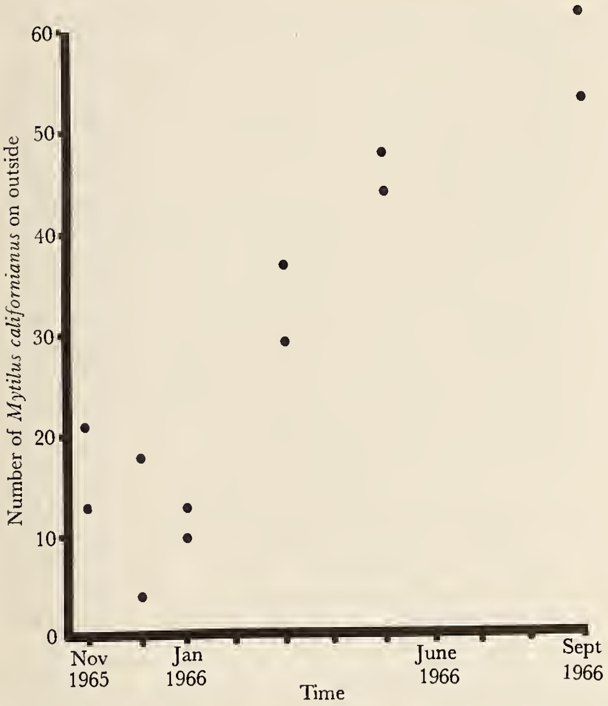

Figure 3

Number of *Mytilus californianus* individuals appearing on the outside of mixed species clumps at successive inspection points of the competition experiment involving juvenile mussels.

the number of *M. californianus* appearing on the outside of the 2 mixed-species clumps at successive inspections. The number increased progressively until the 6th inspection and thereafter remained almost constant (numbers after the 6th inspection were not plotted). This, together with the large size which *M. californianus* attains, would seem to constitute the mechanism by which *M. californianus* finally overgrows *M. edulis* and incorporates the latter into the matrix of the mussel clumps.

Competition Experiments Involving Small Mussels at Santa Barbara Harbor

All cages in the harbor received heavy settlements of *Mytilus edulis* between April and September 1966 (5 or 6 *M. californianus* recruits per cage were also discovered at the first inspection, but not thereafter). The pure *M. californianus* population and the mixed-species cage received 128 and 196 *M. edulis* recruits, respectively, during the month of April. In May these recruits were measured and returned to their respective cages. From this point, both cages containing *M. californianus* must be regarded as mixed-species cages. As the experiment proceeded, the number of *M. californianus* in the cages progressively diminished until at the last inspection (16 months) the populations had been reduced to 10% of the original numbers. This progressive elimination of *M. californianus* was caused by the presence of small *M. edulis* clustering over the outside of the clumps. A large amount of silt settled out from the still harbor waters into the clumps and formed a heavy glue-like mud in the center that apparently smothered the mussels in the middle (Harger, 1968).

Competition Experiments Involving Adult Mussels at Ellwood Pier

Since small mussels exhibit growth patterns differing from large mussels, each population of mussels was divided into 2 groups for the purpose of analysis. The first was comprised of all mussels originally smaller than 4 cm, and the second of those larger than 5 cm. Mussels between 4 and 5 cm were not included in order to make a clear distinction between small and large animals. The "middle-sized" mussels may be regarded as "fill" within the various clumps.

In the case of the small size class, *Mytilus edulis* developing on the outside of population cages placed at lower levels grew significantly faster than *M. edulis* which were started off, mixed evenly with *M. californianus,* enclosed by *M. californianus,* or even in cages containing only pure *M. edulis* ($p < 0.01$, Harger, 1967, table 50). (This difference was detected by an *a priori* single degree of freedom test based on the previously established fact that juvenile mussels on the outside of clumps grow faster than those on the inside.) This observation implied mussels deliberately placed on the outside of cages were probably more favorably oriented than those which had had to crawl through a group of *M. californianus.* Again, as for the juvenile populations, pure *M. edulis* populations showed lower overall growth than *M. edulis* from mixed cages. There was no significant overall difference among the various treatments imposed on the six month *M. edulis* populations set at the upper piling level. However, for the 12-month interval, *M. edulis* populations set up on the outside of mixed groups in the top cages showed significantly more growth than those treated otherwise ($p < 0.001$, Harger, 1967, table 59).

In the 6-month group *Mytilus californianus* individuals placed initially on the outside of the clumps grew significantly faster in upper cages (but not the lower ones) than animals from other treatments ($p < 0.001$, Harger, 1967, table 52). At both upper and lower levels *M. californianus* grew more slowly when developing by itself than when in the company of *M. edulis* ($p < 0.05$, Harger, *ibid.*, tables 52 and 53). (The *a priori* justification for this last comparison was obtained from the previously reported competition experiments involving juvenile mussels, where it was found that *M. californianus* inhibited itself to an extent greater than the extent of the inhibition imposed by *M. edulis.*)

For larger mussels of both species, analysis indicated that the original treatments were not associated with differences in amount of growth for either top or bottom cages for both the 6- and 12-month intervals (mussels immersed for 12 months of course grew more than those immersed for 6 months).

(a) Effects of Enclosure on Growth

It would seem that evidence of competition which could be revealed by differing growth rates was masked by movement of *Mytilus edulis.* An attempt was made to counter this behavior by containing groups of *M. edulis* in small cheesecloth bags which were then placed in the center of *M. californianus* clumps. Unfortunately, the cloth rotted too quickly, thus allowing the *M. edulis* to crawl to the outside of the experimental cages before the clumps became solidly bound up with byssal threads.

Although mussels originally arranged within the cage clumps became displaced as a result of the re-arranging process undertaken by *Mytilus edulis,* some individuals of both species were trapped inside the clumps. In cages immersed for 6 months, the "outside" mussels were separated by spray painting (in this and later sections, the term "inside" mussels refers to individuals selected in this manner). Pure species populations yielded from 10 to 20 such "inside" mussels per cage. Mixed-species treatments provided from 5 to 10 inside *M. californianus* individuals and 0 to 5 *M. edulis* per cage.

(b) Mussels from Bottom Levels

Mytilus californianus and *M. edulis* individuals from inside both the mixed- and pure-species clumps grew less than those on the outside of the same clumps ($p < 0.01$, Harger, 1967, tables 70 - 72). There was no significant difference between growth of *M. californianus* individuals from inside the pure clumps when compared with those from inside mixed-species clumps. On the other hand, *M. edulis* individuals from the inside of mixed-species clumps grew less than individuals from pure-species clumps ($p < 0.01$, Harger, *ibid.*, table 73).

The overall goal in the experiment involving the use of small cheesecloth sacks, designed to retain artificially set "inside" populations of mussels in place, was not achieved; however, growth increment of individual *Mytilus edulis* retained inside the clumps was significantly lower than those on the outside ($p < 0.001$, Harger, 1967, table 74). Growth of small *M. edulis* is reduced by an amount significantly greater than that of large mussels, as a result of developing inside the clumps in all treatments. This is also true of *M. californianus.* Using information from the above described experiments, the percentage growth reduction experienced by a 3 cm mussel resulting from enclosed growth was:

for *M. californianus* growing within pure *M. californianus* clumps	46.02%
for *M. californianus* growing within mixed-species clumps	44.76%
for *M. edulis* growing within pure *M. edulis* clumps	27.50%
for *M. edulis* growing within mixed-species clumps	47.48%
for *M. edulis* growing within mixed-species (cheesecloth) clumps	60.64%

Of the two species, *Mytilus edulis* is most sensitive to development in mixed species associations. Growth reduction for *M. edulis* is relatively slight as the result of developing inside clumps of its own species, but much greater when *M. californianus* is incorporated into the clump matrix.

(c) Mussels from Upper Levels

Growth of mussels confined to the center of the upper cages was reduced approximately the same amount (when compared to that of the outside mussels) as that for the bottom cages ($p < 0.001$, Harger, 1967, tables 76, 77). Categories involving pure- and mixed-species populations for top cages were dispensed with when examining growth of *Mytilus edulis,* since it was impossible to identify sufficient "inside" mussels from these groups.

The "mixed" and "pure" categories were retained for the analysis of growth increment of *Mytilus californianus* on the inside and outside of the upper cage clumps. Again, growth was significantly less for the inside mussels. No significant difference could be detected between *M. californianus* individuals confined within pure-species cages and those within mixed cages.

The percentage growth reduction attributable to development within both mixed and pure clumps taken together (upper level) for *Mytilus edulis* (calculated for a 3 cm individual) was 42%, which is similar to that shown by those inside the lower clump group (see above). *Mytilus californianus* growing on the inside of mixed-species clumps suffered 45% reduction, and within the pure-species clumps 34% reduction in growth. However, these reductions are relative to the growth shown by the adjacent outside mussels. The actual sizes of the inside mussels providing data for these last 2 percentages are not significantly different from one another. The disparity between the 2 values results from the fact that mussels developing on the outside of the "pure" cages did not grow as much as those on the outside of the mixed cages. The growth of the internal "pure" *M. californianus* mussels was 50% less than the outside individuals from the mixed cages. This also indicates that effects of competition by *M. californianus* individuals on themselves are greater than are effects imposed by individuals of *M. edulis*. An individual of *M. californianus* on the outside of a clump and surrounded by *M. edulis* individuals evidently experiences a far less rigorous environment than when surrounded by members of its own species.

Competition Experiments Involving Adult Mussels at Santa Barbara Harbor

Mussels of both species under 4 cm in length grew at the same rate in the pure- and mixed-species clumps. The 4 to 5 cm mussels were included in the "large" group, since the total number of animals used was considerably less than at Ellwood Pier, and it seemed advisable to use all available data. In the "large" group, *Mytilus edulis* grew faster in pure culture than in mixed ($p < 0.05$); however, *M. californianus* showed no difference in growth from these 2 treatments.

OTHER EVIDENCE FOR COMPETITION

Check Rings as Evidence for Competition

The frequency of check rings on a mussel shell may be used as an indication of the degree to which factors, such as wave impact, may adversely affect these animals. An increasing number of check rings is an indication that such a factor (or factors) is increasing in effect. Increasing check ring frequencies occur on mussels from low to high intertidal position, with increasing exposure to wave impact and inside mussel clumps as opposed to outside (Harger, 1970a). In colder climates, annual check rings may be laid down (Seed, 1969a), but no evidence of this was found in the Southern California population.

Frequency of check rings on mussels in the bottom cages from the six-month group were analyzed. When growing with *Mytilus californianus, M. edulis* individuals possess more rings per length of new growth than when growing alone; those growing on the inside do not have a significantly greater number of rings than those on the outside. However, those growing inside mixed populations possess more rings than those inside pure *M. edulis* clumps ($p < 0.001$, Harger, 1967, table 78).

Results for *Mytilus californianus* are less easily interpreted; however, the following trends are separated:
(1) Those individuals inside the clumps have more rings per unit length. This is true for the overall comparisons and for the pure and mixed populations separately.
(2) There is no difference, in terms of the number of rings per unit shell length, between individuals growing inside pure clumps and those inside mixed-species clumps (Harger, 1967, table 79).

Evidence for Competition Obtained from "Dry Body Weight" Data

Data obtained from the cages left in place for the 12-month period indicated that *Mytilus edulis* from both top and bottom cages possessed heavier body weights when growing in pure culture cages as opposed to those from mixed-species cages ($p < 0.001$, Harger, 1967, tables 81, 82). For *M. californianus* growing in the bottom cages, no significant difference in body weight could be detected between those mussels growing in pure cultures and those in mixed-species cages. Results from the top cages indicate that mussels from pure *M. californianus* cages were heavier than those from mixed-species cages ($p < 0.001$, Harger, *op. cit.*, table 84). *Mytilus californianus* from top cages show no significant changes in body weight when growing inside or outside mussel clumps.

Body weight comparisons between mixed and pure populations of both species growing in Santa Barbara Harbor indicated no significant differences between these treatments (body weight provided by both species from the Ellwood Pier lower cages were significantly higher than those within the Harbor cages [$p < 0.001$, Harger, 1967, tables 88, 89]).

When total growth increment data obtained from mussels growing in bottom cages were examined, it was found that *Mytilus californianus* did not reduce the growth of *M. edulis* in mixed-species populations (see above). However, there was a significant reduction in body weight of *M. edulis* growing with *M. californianus* (when compared with weights achieved when growing in pure culture). This reduction was 33% in top cages and 58% in the bottom cages. When growing with *M. edulis,* the reduction in body weight for *M. californianus* is not significant in the bottom cages, whereas in the upper cages reduction was 10% and significant (Harger, *op. cit.*, table 91).

Evidence for Competition Based on Mortality of Mussels Within the Adult Cage Experiment

(a) ELLWOOD PIER

At Ellwood Pier, mortality fell most heavily upon *Mytilus edulis.* For the 6 month period August 1965 to February 1966, 76 *M. californianus* and 127 *M. edulis* were recovered dead from 28 cages (top and bottom only). This discrepancy between the two species was even greater for the 12 month interval, where a total of 90 *M. californianus* and 374 *M. edulis* were recovered from 21 cages.

For both species the number of dead mussels did not significantly differ between the top and bottom positions for the first 6 months. At the end of 12 months this was again true for *Mytilus californianus,* but this time *M. edulis* had a significantly larger proportion of its dead occurring within the top cages (Table 1A); indeed, the large increase in mortality of this species was owing almost entirely to a greater proportion of animals dying in top position. It is probable that these mussels were killed by the heavy storms which the area experienced between late December 1965 and the end of February 1966. The 6-month cages were removed from the pier during February 1966 and at that time many of the *M. edulis* within the top cages were in very poor condition, the flesh of the mantle lobes appearing quite thin and parchment-like. Unfortunately, a laboratory accident prevented retention of body weight records. By the end of the second week in March 1966, large numbers of *M. edulis* in the upper cages of the 12-month group were dead. In addition to this circumstantial evidence, I have shown that growth of

Table 1

Differences between mortality suffered by *Mytilus edulis* and *Mytilus californianus* under differing experimental conditions (see text for explanation)

Test Identification	Group	Observed Mortality	Original Complement	Goodness of fit χ^2, 1:1
A	August 1965 to February 1966			
	Mytilus edulis, top	282	450	
	Mytilus edulis, bottom	97	450	90.30***
	Mytilus californianus, top	33	450	
	Mytilus californianus, bottom	50	450	N. S.
B	*Mytilus californianus,* pure, top	25	270	
	Mytilus californianus, mixed, top	17	405	6.85**
	Mytilus californianus, pure, bottom	24	270	
	Mytilus californianus, mixed, bottom	10	405	13.28***
C	*Mytilus edulis,* pure, top	15	180	
	Mytilus edulis, mixed, top	56	405	6.20**
	Mytilus edulis, pure, bottom	10	180	
	Mytilus edulis, mixed, bottom	46	405	N. S.
D	August 1965 to August 1966			
	Mytilus edulis, pure, top	129	180	
	Mytilus edulis, mixed, top	153	270	3.929*
E	*Mytilus californianus,* Harbor, mixed	42	90	
	Mytilus californianus, Harbor, pure	48	180	7.41**
F	*Mytilus californianus,* Harbor, small	67	135	
	Mytilus californianus, Harbor, large	23	135	21.50***

M. edulis is restricted by moderate wave shock (Harger, 1970a) and that *M. edulis* is more susceptible to effects of intertidal exposure than *M. californianus.*

Two further items of evidence supporting the contention that competition occurs between adult populations of the two species emerge from the 6-month mortality data. First, at both upper and lower levels, mortality of *Mytilus californianus* in pure *M. californianus* population cages was significantly higher than in the mixed-population cages (Table 1B). Second, mortality of *M. edulis* populations growing in the mixed cages at the top level was significantly greater than that occurring within pure *M. edulis* populations (Table 1C); this was not so for the bottom level, however.

There was no significant difference between deaths in pure culture *Mytilus edulis* or *M. californianus* between the upper and lower cages.

These results may be accounted for in the following manner: selection against mussels which are intolerant of crowding and squeezing, etc., is probably high in a pure *Mytilus californianus* clump, since the physical characteristics of this species promote formation of solid, tightly bound clumps. The comparatively loose clump structure which is formed when *M. edulis* is incorporated into a mass of mussels undoubtedly relieves pressure on all members; hence, *M. californianus* has lower mortality in such a matrix. Conversely, the addition of *M. californianus* to a group of *M. edulis* considerably strengthens the resulting clump. *Mytilus californianus* individuals anchor their strong byssal threads to any surface they can reach, including members of the other species, which may then be drawn closely together; this perhaps reduces the efficiency of feeding. I recovered several specimens of *M. edulis* from the mixed-species cages which, though yet alive, were incredibly twisted and distorted, some with pieces gouged from the edges of the shells revealing gaps partially cemented in and others with cracked hingelines. I often found, in the course of disassembling mixed clumps, specimens of *M. californianus* growing in such a manner that the sharp posterior end of their shell projected onto the posterior end of individual *M. edulis.* In such cases, a definite notch had been carved into the shell of *M. edulis* by that of *M. californianus.* Therefore, I have no hesitation in stating that competition does occur between adult populations of the two species. Field evidence indicates this to be the case and information obtained from experiments is sufficient to lend substantial backing to the claim.

Table 1D shows, for the 12-month group, evidence that *Mytilus edulis* growing with *M. californianus* suffered lighter mortality than when growing alone in the upper cages. This difference was associated with the extremely heavy mortality incurred by this species in the top cages. Of 450 individuals set out, 375 died; harsh environmental conditions could have been responsible for this mortality, which may have been eased somewhat by the presence of *M. californianus* individuals sheltering *M. edulis* (Harger, 1970c).

(b) SANTA BARBARA HARBOR

Similar mortality was suffered in this location by each of the two species (90 *Mytilus californianus,* 87 *M. edulis*). Mortality within the pure and mixed populations of *M. edulis* did not differ and there was no difference in the mortality of small and large mussels (small mussels are, in this case, defined as individuals smaller than the median length for each species in each cage).

Mortality in *Mytilus californianus* populations, however, was significantly higher in mixed culture than in pure (Table 1E). Further, in both pure- and mixed-species clumps, more small individuals died than did large (Table 1F). This disparity in the mortality of the two size classes may be understood if it is recalled that in pure *M. californianus* clumps the juveniles tend to occur within the center. In the harbor, silt settlement builds a filling of thick mud within the clumps (Harger, 1968, 1970b); this undoubtedly killed the smaller mussels. Large mussels simply project from centers of clumps and therefore tend to be clear of contained mud. *Mytilus californianus* developing in mixed-species clumps will usually be left in the center as *M. edulis* crawls to the outside of the clumps.

The EFFECT of PREDATION on *Mytilus edulis* and *Mytilus californianus*

Mussel predators abound in all locations discussed in this study. No fewer than 9 invertebrate predators exhibit a preference for *Mytilus edulis* to *M. californianus.* These are: two species of sea stars, *Pisaster giganteus* (Stimpson, 1857) and *P. ochraceus* (Brandt, 1835) (Landenberger, 1968); 5 species of muricid gastropods, *Thais emarginata* (Deshayes, 1839) and *Acanthina spirata* (Blainville, 1832) (W. Murdoch, personal communication), *Ocenebra poulsoni* Carpenter, 1864, *Ceratostoma nuttalli* (Conrad, 1837), and *Jaton festivus* (Hinds, 1843); and finally 2 species of crabs, *Cancer antennarius* Stimpson, 1856 and *Pachygrapsus crassipes* Randall, 1839 (a third species of crab, *Pugettia producta* (Randall, 1839), eats few mussels and shows no preference). Preferences for the last 5 species mentioned above were determined in the laboratory (Table 2A, 2B, 2C, 2D, 2E, 2F), although for most species field evidence also substantiates these findings.

Investigation of the competition experiment involving small mussels set in varying proportions at Ellwood Pier indicated that cages containing higher proportions of *Mytilus edulis* supported a higher concentration of crabs (*Cancer antennarius*) (Figure 4). In these cages predation had fallen most heavily on *M. edulis,* as shown by the large number of fragmented *M. edulis* shells present. As the experiment proceeded, such selective predation reduced the proportion of *M. edulis* in each cage. The 4-month interval between check periods was apparently sufficient to allow crab zoeae to settle from the plankton and to grow inside the cages to a maximum recorded carapace width of 3 cm. The shorter inspection time interval used in the first experiment dealing with small mussels, apparently allowed crabs insufficient time to enable them to reach a size where they could prey on the caged mussels. Disturbances at each inspection time eliminated small crabs as the mussels were cleaned for measuring.

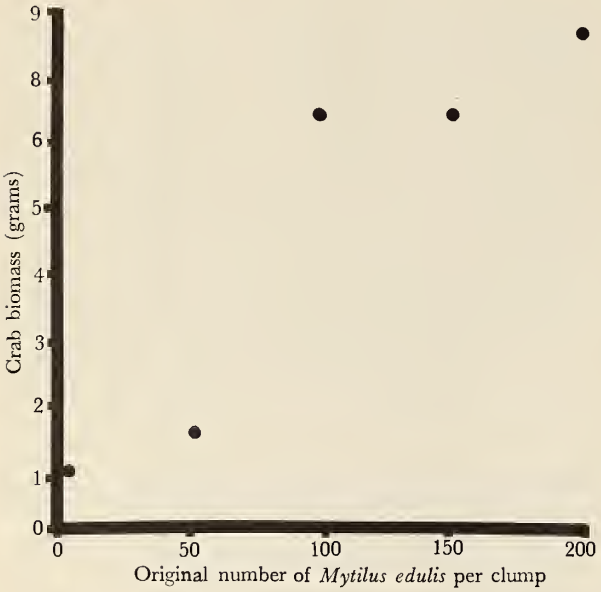

Figure 4

Relationship between biomass (wet weight of crabs) and original number of *Mytilus edulis* set within population cages at Ellwood Pier (January 1966 to May 1966).

Mytilus edulis taken from clumps infested with *Thais emarginata* can be identified as having been attacked by this snail by the presence of radula holes made by the predator. A sample of dead shells collected from a mixed-species clump indicated that in natural populations a preference is shown for *M. edulis* (Table 2G). In the laboratory this preference was so strongly exhibited that *M. edulis* was almost entirely eliminated from a clump of mussels composed of both species before *M. californianus* was attacked to any appreciable extent (Figure 5). The snails do not seem to be selecting mussels on the basis of shell thickness (*M. edulis* shells are thinner), since, when 2 groups of *M. edulis* differing markedly in this character (one group from Ellwood Pier, the other from Ellwood shore) were presented to *Thais,* no significant difference in choice was revealed (Table 2H). Both *Thais* and *Acanthina* prefer *M. edulis* and *M. californianus* to *Septifer bifurcatus* (W. Murdoch, personal communication). Again, neither the way in which the choice is made nor the reason for it are known.

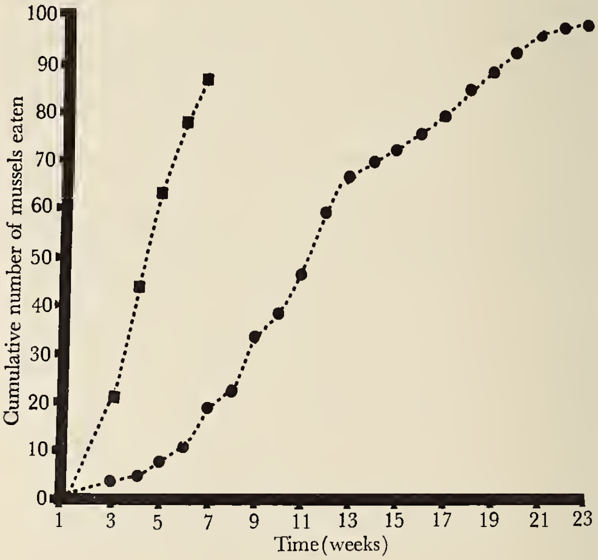

Figure 5

Rate of predation by *Thais emarginata* (20 individuals) acting on a mixed species clump of mussels (maximum size of mussels 4.0 cm in length).

● *Mytilus californianus*
■ *Mytilus edulis*

Of the crabs, both *Cancer* and *Pachygrapsus* prefer *Mytilus edulis* to *M. californianus,* and the latter to *Septifer* (Table 2I). That this choice might be based on the relative shell strengths of the 3 species must now receive more consideration. Figure 6 indicates the maximum size of each species of mussel taken by particular individuals of *Pachygrapsus.* The size of *Septifer* taken by individual crabs is significantly less than for either of the other 2 species. The data do not indicate such a difference be-

Table 2

Relative choices between mussel species made by invertebrate predators

Test Identification	Predator	Replications	Conditions of prey	Prey	Prey eaten	Goodness of fit x^2, 1:1
A	*Ocenebra poulsoni* 20 individuals per treatment (laboratory)	1	26 of each species offered weekly	*M. edulis* (7 week pooled)	49	
				M. californianus (7 week pooled)	6	33.62***
B	*Ceratostoma nuttalli* 8 individuals per treatment (laboratory)	2	20 of each species offered weekly	*M. edulis* (5 week pooled)	51	
				M. californianus (5 week pooled)	13	22.575***
C	*Jaton festivus* 5 individuals per treatment (laboratory)	2	10 of each species offered weekly	*M. edulis* (5 week pooled)	34	
				M. californianus (5 week pooled)	2	***
D	*Cancer antennarius* 1 individual per treatment (laboratory)	6	10 of each species offered in 3-day intervals	*M. edulis* (45 day period)	56	
				M. californianus (45 day period)	25	11.86***
E	*Pachygrapsus crassipes* 1 individual per treatment (laboratory)	7	10 of each species offered in 3-day intervals	*M. edulis* (24 day period)	208	
				M. californianus (24 day period)	131	17.48***
F	*Pugettia producta* 1 individual per treatment (laboratory)	2	10 of each species offered in 3-day intervals	*M. edulis* (54 day period)	34	
				M. californianus (54 day period)	37	N. S.
G	*Thais emarginata* feeding on natural population of mussels (field)	1	355 *Mytilus edulis* living in clump	*M. edulis*	60	
			269 *M. californianus* living in clump	*M. californianus*	29	4.00*
H	*Thais emarginata* 8 individuals per treatment (laboratory)	1	14 of each prey type offered weekly intervals	Thin-shelled *M. edulis* (7 week period)	23	
				Thick-shelled *M. edulis* (7 week period)	23	N. S.
I	*Pachygrapsus* 1 individual per treatment (laboratory)	5	10 of each species offered in 3-day intervals	*M. californianus* (27 day period)	82	
				Septifer (27 day period)	21	22.68***
	Pachygrapsus 1 individual per treatment (laboratory)	4	10 of each species offered in 3-day intervals	*M. edulis* (27 day period)	201	
				Septifer (27 day period)	22	143.64***
	Cancer 1 individual per treatment (laboratory)	3	10 of each species offered in 3-day intervals	*M. californianus* (21 day period)	138	
				Septifer (21 day period)	29	71.14***
	Cancer 1 individual per treatment (laboratory)	3	10 of each species offered in 3-day intervals	*M. edulis* (21 day period)	117	
				Septifer (21 day period)	5	***

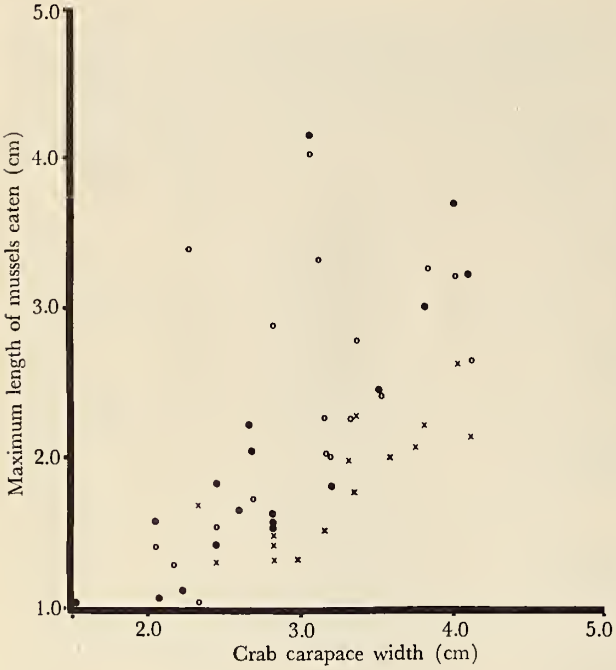

Figure 6

Relationship between maximum size of mussels taken and size of *Pachygrapsus crassipes.*
● *Mytilus edulis*
○ *Mytilus californianus*
× *Septifer*

tween *M. californianus* and *M. edulis.* This is perhaps because *M. edulis,* although the weaker-shelled of the two, has a particularly smooth shell which often "pops" out of a crab's claws when the predator apparently tries to crack it. *Mytilus californianus* is heavily ridged and so may provide a better surface for a crab to grip. Another factor at work here concerns the manner in which mussels may be attacked by crabs over long periods. Over short periods, attacks are made by the simple act of crushing mussels between the chelipeds. However, crabs can be induced to eat progressively larger mussels over long periods by offering large prey exclusively. Under these circumstances the attack pattern becomes modified, and the predator tends to pick pieces from the posterior "siphon" region of the prey until entrance is gained. By this method both *Pachygrapsus* and *Cancer* seem able to open similar sized *M. edulis* and *M. californianus,* provided enough time elapses. *Mytilus edulis* yields readily to attack but *M. californianus* takes a little longer. Figure 6 also shows that an upper mussel size limit exists for each crab size and since *Pachygrapsus* seldom grows above 4.25 cm in carapace width, it follows that mussels above 4 cm are safe from *Pachygrapsus* predation.

Figure 7 shows a similar relationship for *Cancer* crab size and maximum size of mussel attacked. Large *Cancer* crabs (13 cm) can easily crack individuals of *Mytilus californianus* up to 18 cm in length. Small crabs of this genus have a marked effect on the survival of young mussel populations. Figure 8 shows the inverse relationship between the numbers of recruits (both species) found in the 12-month adult competition cages at Ellwood Pier and the number of *Cancer* crabs found in the cages. Small mussels were absent or very rare within cages containing crabs, and extremely numerous within cages free from crabs. Intertidally, *Pachygrapsus* may commonly occur at densities of 1 to 5 per square foot. Subtidally, small *Cancer* crabs occur at similar densities (Table 3). These crabs (2 - 4 cm carapace width) may eat from 5 to 7 individuals of *M. edulis* 1 - 2 cm in length per day and 2 - 4 *M. californianus,* and *Pachygrapsus* of similar size may consume 3 - 9 *M. edulis* (Harger, 1967, table 127).

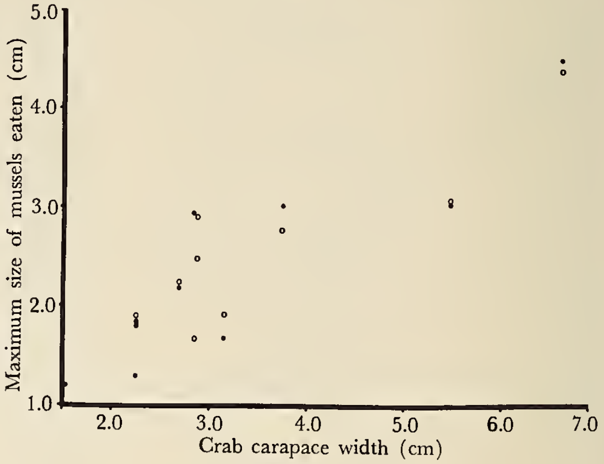

Figure 7

Relationship between maximum size of mussels taken and size of *Cancer antennarius.*
● *Mytilus edulis*
○ *Mytilus californianus*

At least 6 to 8 weeks from settlement are required before the mussels become sufficiently large so that crabs can no longer eat them. In 7 weeks, therefore, 4 crabs eating 5 mussels per day could eat 980 (say 1000) small mussels. Populations of mussels, to survive on most rocky shores inhabited by crabs, must settle at densities in excess of 1000 per square foot. *Mytilus edulis* settles at a rather low rate throughout the year and it is reasonably easy to place out collectors suspended from the pier so that crabs from the surrounding structures cannot crawl onto them. Such collectors invariably gather populations of *M. edulis.* If, however, the same collectors are placed directly against the pier pilings, no populations of mussels are gathered, presumably because crabs from these structures invade the collectors.

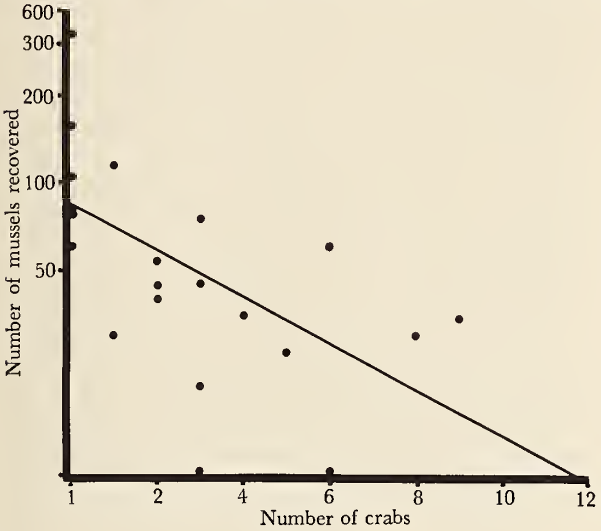

Figure 8

Relationship between number of recruit mussels (both species) recovered from 12 months cages and number of small crabs inhabiting the cages. Regression is significant. $p < 0.001$.

Table 3

Numbers of crabs per square foot occurring at various positions, both intertidally and subtidally

Number of crabs	Area (sq. ft.)	Place	Number of crabs per sq. ft.
Pachygrapsus crassipes			
102	63.0	Ellwood Pier caisson	1.61
412	92.5	Ellwood Pier caisson	4.45
32	1.87	Artificial mussel clump Ellwood shore	17.11
345	324	(Hewatt, 1937) Monterey Bay	1.06
38	4.0	Floats, Santa Barbara Harbor	9.5
43	4.5	Floats, Santa Barbara Harbor	9.55
430	71.5	Dawson, 1963	6.43
Cancer antennarius			
(carapace width 0.5 to 3.5 cm)			
13	2.0	outside of submerged collander Ellwood Pier	6.5
9	2.0	outside of submerged collander Ellwood Pier	4.5
12	1.5	Sample from Ellwood Pier submerged pilings	8.0

During the summer months (May to August) settlement by *Mytilus edulis* increases greatly and it is at that time that most new populations are established (normally, *M. edulis* recruits move to the outsides of the clumps, thus presumably increasing the chance that they will be taken by predators). Settlement of *M. californianus* in both years occurred in the winter months, between August and February. The retiring habits of the juvenile *M. californianus* presumably lessen the probability of predation, since they seem to be comparatively well protected inside the clumps.

In the cages removed after the period August 1965 to February 1966, only 90 *Mytilus californianus* and 1392 *M. edulis* recruits were recorded. Natural clumps dominated by *M. californianus* contain large numbers of small individuals. The low recruitment recorded above suggests that *M. californianus* juveniles occurring within such clumps (Harger, 1968) may enjoy high survival rates and owe their numbers to slow but steady recruitment. *Mytilus edulis,* on the other hand, provides extremely large numbers of recruits, particularly in the warmer months. This in itself might suggest that the concentration of predation on *M. edulis* by these intertidal predators was, in some way, triggered by large predictable settlements.

DISCUSSION AND CONCLUSION

Factors Permitting Co-Existence

Some of the factors allowing the two species to co-exist over much of their range are listed below:

1. A multiplicity of exposure regions such as those at different levels of the beach, at the front and rear of boulders, on pier pilings, on rocks presenting differing frontal aspects to the surf; all allowing differing competitive interactions to take place.
2. A periodicity in occurrence of rough weather: large patches of mussels may be torn from the shore and pier pilings during winter storms, exposing new patches for subsequent colonization.
3. Structural complexity afforded by larger mussel *per se* and by the presence of barnacles on shells of large mussels.
4. Variations in pressure exerted by predators.
5. Species ratio-dependent effect of storms.

Such factors may be included within the general concept of heterogeneity, both in space (nature of the rock substrate, etc), in time (the weather and substrate alterations caused by the growth of the mussels themselves), and in the nature of biological interactions (predation and competition).

The two species co-exist if populations on the coast are viewed as a whole. In any one place, however, during the competitive process one species may be rated as being more successful than the other. Since the environment is far from stable, today's advantage may be tomorrow's drawback: complexity "interpreted" as unpredictability of environmental (meteorological) conditions by the mussels is a necessary component of this co-existence.

Environmental predictability, represented by relative constancy, is approached only at the extremes of shelter and strong wave exposure; in each, only one species is really successful. Production of offspring by *Mytilus edulis* (measured as settled individuals) is much higher than that of *M. californianus,* certainly so during the years 1965-1967. This higher recruitment rate of *M. edulis,* together with the behavior of the spat which crawl out to the most favorable positions for growth, may help it in co-existence with *M. californianus.* Through such behavior, *M. edulis* may approach the situation envisaged by SKELLAM (1951) when he proposed that co-existence might be possible if one species (*M. edulis* in this instance) was better at finding and colonizing new places than the other species, even though that species was eventually beaten during subsequent competition.

At this stage, it might also be interesting to comment on HUTCHISON's (1951) concept of a fugitive species, *i. e.,* one which is specialized in moving into a newly vacated area (as at the start of some successional process) and quickly growing, reproducing, and then going on to another such new area. *Mytilus edulis* in its region of environmental optima (bays) is probably not a fugitive species; however, in the region of overlap, in exposed situations generally, it quite plainly displays fugitive characteristics with respect to *M. californianus. Mytilus edulis* seems to become sexually mature earlier than *M. californianus,* at least laboratory experience indicated *M. edulis* was capable of spawning when 2 - 2.5 cm long and *M. californianus* at 3.5 cm, usually 4 cm.

The immediate outcome of competition at Ellwood Pier between small *Mytilus edulis* and *M. californianus* (1 - 2 cm) is different from that between large individuals (7 - 9 cm). Small *M. edulis* crawl to the outside of any mixed clump and there enjoy a growth rate approximately twice that of *M. californianus.* This advantage may last until the individuals of *M. edulis* are 5 - 6 cm long; by this time, however, they no longer interlock as efficiently as before, and so smaller *M. californianus* are able to protrude between the larger *M. edulis,* with consequent increase in growth rate.

Large *Mytilus edulis* also tend to move towards the outside of clumps; their mobility is much reduced and those that are successful may become dislodged by wave action. Small specimens of *M. edulis* may be dislodged only in regions of extreme wave action; an inverse correlation exists between the amount of exposure and the maximum size of *M. edulis* which can survive by themselves (HARGER, 1970a). This is complicated by the tendency of *M. californianus* to bind *M. edulis* firmly onto the substratum, thus raising the maximum size limit in all but the two extremes of the exposure range (HARGER, 1970c). Individuals of *M. edulis* not successful in moving out of a clump become bound and anchored by *M. californianus* within the body of the clump, their growth rate falls and mortality increases because the weaker-walled *M. edulis* are crushed by their strong-shelled competitors and because growing *M. californianus* probably expand in such a way as to prevent *M. edulis* shells from opening properly. Ultimately, large successful *M. californianus* provide a new substrate for colonization by barnacles and young mussels of both species.

A laboratory species-interaction similar in form to that described above is reported by AYALA (1968, 1971) involving two species of the fruitfly *Drosophila.* In this instance, one species seems to be at an advantage in the larval stage, while the other species is at an advantage in the adult stage. The interaction is frequency dependent and mixed populations of varying proportions show a tendency to converge to constant frequencies, from limited experimental displacement, so establishing a stable equilibrium. The husbanding program (serial replication) involves simplification of the total potential interactive regime between the two species, however all stages of the life cycle are involved, whereas only the sessile stage is involved for *Mytilus edulis* and *M. californianus.* An additional difference is that separate environmental resources are exploited in *Drosophila* by larvae and adults, whereas, in effect, the same resources are competed for by juvenile and adult mussels.

It is apparent that competition proceeds in different ways according to the size (and frequency) of the individuals involved. Advantages fluctuate between the two species both in space and time, being modified by predation and by aspects of the physical environment. In many instances, if *Mytilus californianus* alone were present, wave action could not readily dislodge large numbers of animals, thereby leaving wide areas of bare rock for recolonization. The presence of *M. edulis* may lead to the elimination of large numbers of *M. californianus* during storms (HARGER, 1970c); however, storms also exact their toll on populations consisting only of *M. californianus* in a density-dependent manner (HARGER & LANDEN-

BERGER, 1971; see also SEED, 1969). After even the heaviest storms, some patches of both species remain and, since breeding takes place throughout the year, these can then seed new areas. In the last analysis, each species has its own exclusive refuge, though whether decisive use of this is ever made is hard to decide.

At intermediate points between the two extremes of exposure, varying proportions of *Mytilus californianus* and *M. edulis* are found. It seems that even though competition can be demonstrated between the two species, competitive elimination of one by the other is rare in intermediate environments. The relative numbers of both species at any point in the region of overlap probably could be predicted from a continuous knowledge of settlement density, weather conditions and predatory pressure, in that order.

The field evidence (dead *Mytilus edulis* shells) indicates that in regions such as represented by Ellwood Pier, *M. californianus* in some instances has virtually eliminated *M. edulis* from what must have been mixed aggregations. There are, however, many separate populations on the pilings, each being different from the others in make up (HARGER & LANDENBERGER, 1971). It is because there are so many different populations that *M. edulis* is always ensured of conditions favoring survival.

A model of this system necessarily assumes that changes in the mode of action of the weather and predation prevent competitive exclusion by continually modifying advantages enjoyed by each species in different geographical locations. All the active relationships involved have yet to be quantified; nevertheless, the assumption of change in either, or both, wave action and predation pressure in locations outside extremes of shelter and exposure, coupled with variations in proportional representation of species in clumps together with variation in size and age of constituent individuals, provides an infinitely variable background from which co-existence emerges by way of different pathways.

In the light of evidence from this study, how much importance may we assign to the effects of competition on the evolutionary process? Plainly, all traits which I consider to be important in competitive interaction between these two species appear to be primarily adaptations to the physical environment. *Mytilus edulis* crawl out from the clumps and so escape burial by silt. The very strong byssal threads and thick shells of *M. californianus* have obviously evolved in connection with its ability to withstand heavy wave impact. The main advantages possessed by each species can thus be tied to environmental influences.

Competition and the Theory of the "Niche"

The basic concept of a "niche" as being associated with dissimilar requirements of different bird species was put forward by GRINNELL (1904). ELTON (1927) advanced the following description: "It is convenient to have some term to describe the status of an animal in its community, to indicate what it is doing . . . the term used is niche. The niche of an animal means its place in the biotic environment, its relation to food and enemies."

As originally conceived, this was a rather loose definition, since ELTON (*op. cit.*) goes on to say: "There is often an extraordinarily close parallelism between niches in widely separated communities. In the arctic regions we find the arctic fox, which, among other things, subsists upon the eggs of guillemots, while in winter it relies partly on the remains of seals killed by polar bears. Turning to tropical Africa, we find that the spotted hyaena destroys large numbers of ostrich eggs, and also lives largely upon the remains of zebras killed by lions. The arctic fox and the hyaena thus occupy the same niches – the former seasonally and the latter all the time."

HUTCHINSON (1957) generated a useful abstraction in picturing the niche as an n-dimensional hypervolume defined by the upper and lower values of a series of coordinates which represent a set of environmental variables that will permit maintenance of a "steady state" population of a particular species. As SLOBODKIN (1961) remarks, "This permits an unequivocal statement of what we would like to mean by an ecological niche, it has several practical difficulties."

MCNAUGHTON & WOLF (1970) comment to the effect that most of modern niche theory derives from efforts to relate the competitive exclusion principle to Hutchinson's n-dimensional niche. Indeed, much abstract theorizing concerning the nature and modes of determination of the niche has been expended on what would appear to be little concrete data; certainly, most analyses scarcely begin to approach the complexity of the problem.

The attempts of MACARTHUR & LEVINS (1964, 1967), LEVINS (1968) and MACARTHUR (1968) to develop a theoretical framework embracing a quantitative formulation of aspects of HUTCHINSON's (*op. cit.*) niche incorporating responsive elements as dictated by competitive processes unfortunately suffer from the use of the entirely abstract notion of environmental grain size. MACARTHUR (1968) outlines this concept of environmental structure proposed by himself and LEVINS (1964) as follows: "We now call a patch of environment 'fine grained,' relative to species, if that species comes upon the resources and other components of that patch in the proportion in which they occur. Conversely, if the species can spend a disproportionate amounts of time in one resource or the other component, we call the patch 'coarse grained'."

Inasmuch as such a classification is dependent on the mode of encounter of mixed resources realized by particular organisms (for whom the classification is relevant), it seems unsound to propose that any organism – the presumed result of natural selection – should encounter mixed resources in the proportion in which they occur naturally. Many studies indicate that predators exhibit distinct choice when actively feeding on several species (Allen, 1941; Ivlev, 1961; Landenberger, 1968). As previously mentioned, sea stars actively choose *Mytilus edulis* over *M. californianus*; furthermore, *Pisaster ochraceus* may actively modify its hunting behavior by experience (Landenberger, 1966, 1968). To claim that a real environment can be assembled from building blocks of fine-grained patches (MacArthur, 1968) is tantamount to denying the action of natural selection. In all, these analyses serve to indicate that multiple-resource environments support multiple species by specialization in a one-to-one relationship, a conclusion that differs little from that of Williamson (1957).

The distinction made between co-existence within fine-grained environments by virtue of resource subdivision (MacArthur, 1968) must logically coalesce with coarse-grained subdivision or habitat specialization, since natural selection would favor recognition of component resources if a successful competitor were to intrude upon a single organism utilizing fine-grained perception (presupposing such an organism could exist). In this regard the axiom of inequality means that the grains or individual constituents of a resource cannot, in fact, be equal to one another. If such constituents are taken as perceptually equivalent, this indicates that no selective advantage can accrue to an individual organism if it adopts tactics which subdivide the resource as to category. Even the example quoted by MacArthur & Levins (1964) and again by MacArthur, (1968) whereby seed dispersal in a plant may be fine-grained but adults arising from successful germination exist in a coarse-grained fashion, must also suffer from the logical consequences of perception. On the one hand, seed dispersal by any plant is less than likely to be random with respect to environment, except possibly in small localized areas; of course, such areas themselves are probably functionally related to parent stock. On the other hand, successful germination may itself be viewed as a form of biological perception.

As MacArthur (1966) has conceded, ideas of communities structured on the "broken stick" model should be discarded. In this regard, the work of Cohen (1966) dealing with an abstraction of competitive theory based on random assignment provides comfortable models in terms of such postulates, in the sense that some carefully selected communities can be shown to mimic resultant expected distribution of individuals per species (see Miller, 1967, for a useful discussion of this point). This, however, provides no realistic description of the operation of competitive interactions. There is no reason to suppose either that relative competitive ability of organisms in a community can be measured across one gradient or, in those rare cases where this might be possible, that such ability should be distributed among species according to any regular function. On the contrary, selection is likely to determine simple changes in structure and function which remove organisms from each other, in terms of competitive ability, by orders of magnitude. Hence dominance is to be expected in organisms particularly suited to any environment. A simple example would encompass the development of rudimentary light perception. In the species interaction under consideration, the principal obvious adaptations shown by *Mytilus californianus* enabling that animal to successfully utilize areas of heavy wave impact to the exclusion of *M. edulis* are development of thick reinforced shells, strong byssal attachments and conservative mobility characteristics. None of these characters is of particular value in quiet waters, yet all appear to be comparatively minor differences from homologous characters in *M. edulis*.

If generalization can be extracted from the example reported here, niche overlap may be widespread and variable in nature because the existence of competition need not necessarily lead directly to the phenomenon of competitive exclusion (see Miller, 1967), notwithstanding the suggestion by Cole (1960) to the effect that genes favoring reduction in competitive interactions should be selected for.

The use of n-dimensional space to describe requirements of a particular species in isolation from its competitors, predators, etc., is unsatisfactory, principally because this leads to a description of the potential habitat of an organism. Plainly, each different community in which a particular species occurs will result in a different realized niche for that species (see Miller, 1967). Differing sets of circumstances in association with the species representation constituting the community in which a given organism finds itself will modify the successful response of that organism.

Since we are presumably dealing at all times with evolving, and therefore changing, systems (species, species associations, communities, etc.), it is unlikely that there exists a static and definable niche, except as is represented by a particular species' distribution from time to time. Any attempt to rate environments in terms of their overall importance to a particular species (McNaughton & Wolf, 1970) without reference to all possible conjunctions of circumstance, taking into account such seemingly unimportant locations, habitats, areas, etc., as may determine species survival in rare instances, should be regarded with suspicion.

Are bays more important to *Mytilus edulis* than semi-protected shorelines, pier pilings, natural vertical stacks, or even exposed shores? In favorable circumstances, *Mytilus edulis* is undoubtedly represented more profusely outside bays than inside. Such an increase in population size extends opportunity for appearance of new genetic material (by recombination or *de novo*) ; the ability to colonize and recolonize distant locations must also be increased. In short, access to the area outside the harbors becomes an asset evolutionarily valuable to the species (see Carson, 1968, for a discussion of the consequences of a population "flush"). Under extremely unfavorable circumstances, *i. e.*, heavy storms, intense predation, etc., *M. edulis* could be driven back almost to the confines of the harbors. Quite plainly, both habitats are of importance to this animal – no one area can be said to be more important than another. Harbors, the apparent refuge for *M. edulis*, also have drawbacks by way of increasing pollution.

Contained in the idea of niche seems to be a notion of the necessary principal components of existence, *i. e.*, those requirements which must be met in order that an organism may successfully reproduce consistently. In a sense, this is the essence of Hutchinson's (1957) fundamental niche, which utilizes maintenance of steady state population as a definite central criterion.

A simple model of competition in the field would suppose that displacement would occur whenever any portion of such components are overlapped by a competitively superior organism. Maintenance of co-existence in competitive associations of two or more species would thus depend on one or the other (or a combination) of two mechanisms:

(1) Each species involved in competition by virtue of overlap in ecological requirements must enjoy a realized niche of greater extent than defined by its principal components, thus allowing plasticity in responses to its competitors.

(2) Since different species are, by definition, exposed to differing selective forces, an oscillating balance in the direction of the suggestion by Pimentel *et al.* (1965) might be struck between a selective response to primary environmental factors and competitive ability as expressed towards a competitor.

For instance, the necessity to retain byssal holding strength and stability of behavior as far as limiting movement is concerned for *Mytilus californianus*, could be balanced by a selective response towards greater mobility in order to compete effectively with *M. edulis* in regions of moderate water movement. As well as this, intra-specific competition among *M. californianus* individuals may also lead to greater mobility. Successful competitors might well be eliminated by severe storms. The same process in counter-action might also be at work in *M. edulis* populations. At some point along an environmental gradient, tight byssal threads may be advantageous in rough water, perhaps even serving to preserve a competitive advantage over *M. californianus*; however, such characteristics might well be detrimental to survival in a quiet muddy environment, leading to tight clumps which could result in the suffocation of constituent individuals through accumulation of mud.

In most laboratory studies involving competing species, the principal components of the niches of interacting species are both constrained by, and to some extent determined by, the universe adopted. In such situations, either food or space or both are immediately limiting factors, usually acting in a simple manner. De Bach (1966) correctly indicates that for practical purposes, either food or space or both can be used to define a niche. In a natural environment, however, both components are subject to infinite subdivision and may be expressed in variable interaction throughout the range of competing species.

Ayala (1968) notes in laboratory populations of *Drosophila* that the size of a population living in a certain environment depends upon its genetic constitution and that further in the case of mixed species populations sharing the same resources, the numbers of each species depend on the genetic constitution of the competing species as well.

Basically, the overall genetic constitution of an organism (its gene pool) determines its potential niche. For any set of circumstances comprised of biological factors (predators and competitors) in conjunction with physical factors, a subset of principal niche components may be defined, dependent on local gene pools. The total representation of such subsets at any moment in time throughout the range of a species determines a restricted definition of the fundamental niche of that organism. Logically, this may be expanded to include regions wherein a truly steady state population may not theoretically be retained by utilization of the contained resources, yet nevertheless, immigration from regions of over-production may support an essentially steady state population or introduce the genetic basis for successful maintenance.

The ability of an organism to meet requirements imposed by future environments is (under the influence of natural selection) determined by the successful reproduction of current gene pools and the extent to which information gathered by way of experience with past environments is retained within its overall genetic constitution. In this regard, it may be appropriate to define environmental stability by way of the ability of a species to deal successfully with such natural variability as may occur, through maintenance of viable populations. The fundamental niche, like "population equilibrium level" (Harger & Landenberger, 1971), can only be defined in terms of an organism's history and the environment in which it finds itself.

In dealing with the determination of niche breadth, Levins (1968) indicates that abundant species are usually the ones which are broad-niched. He concludes that a broad niche is optimal in an environment which is uncertain. In connection with this, Ayala (1968), using *Drosophila,* provides laboratory evidence indicating that artificially increased genetic diversity results in higher population sizes than are maintained by normal unmodified stocks. McNaughton & Wolf (1970) believe that genetic diversity determines niche width. They state that it seems likely that the greater niche width of more abundant species would, in fact, be driven by their greater abundance. Unfortunately, the seeds of circularity are contained here, because the question of determination of factors permitting the expression of abundance is not dealt with satisfactorily. By this argument, genetic diversity accruing from abundance can reinforce abundance, but not determine it in the first instance. They maintain that there are two possible mechanisms responsible for determination of niche width:

1. relative efficiencies at exploiting critical limiting factors,
2. frequency and carrying capacity of the exploitation speciality.

I have argued previously that the only appropriate practical measure of niche width is some function of species representation. For a realized niche, this may be expressed as (1) total area inhabited over a given time interval; (2) total numbers over a given time interval.

On a world-wide geographical dimension, *Mytilus edulis* has by far the broader niche of the two species. It would seem that its success is due principally to a combination of both previously quoted alternatives. However, it is apparent that adaptation has been primarily in response to physical (environmental) characteristics; therefore, frequency and carrying capacity of the exploitation speciality stand as the primary determining factors. *Mytilus edulis* also falls into the category of being adapted to variable habitats, and thus has a broad niche and is dominant, as Levins (1968) expected. The degree of overlap expressed by the two species is determined by relative efficiencies at exploiting critical limiting factors, as well as the extent to which those factors are represented. These efficiencies appear to be under constant and persistent selection pressure as immediately unpredictable variation in both environmental and biological factors interact. *Mytilus californianus,* although by definition possessing a niche of reduced breadth in comparison to *M. edulis* on a world-wide basis, nevertheless is just as successful – perhaps more so – when compared with its competitor on the scale of the Pacific West Coast of North America, as far as both the area of distribution and numerical representation are concerned. The niches of both species for this last mentioned region can be described as approximately equal but varying volumes intersecting by changing degrees temporally.

ADDENDUM

In order to avoid the expense involved in publishing tables, few of the data gathered as part of this investigation are recorded in this paper. All experimental analyses referred to, as well as additional information, can be found in the thesis from which this paper is abstracted (Harger, 1967), available on University Microfilms no. 69-1719, 300 North Zeeb Road, Ann Arbor, Michigan 48103. A set of summary tables may be obtained from the author on request.

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